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# *Pholiota olivaceophylla*, a forgotten name for a common snowbank fungus, and notes on *Pholiota nubigena*

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Abstract — A name has been found for a common species in *Pholiota* subg. *Flammuloides* fruiting during and soon after snowmelt in the subalpine *Abies* forests of California: *Pholiota olivaceophylla* is characterized by rather pale slime-covered basidiocarps, relatively pale brown ellipsoid to slightly phaseoliform spores, 6.0–8.5 × 3.5–5.0 µm, with an inconspicuous germ pore, and abundant lageniform pleurocystidia. The ITS sequence of the type collection of *Ph. olivaceophylla* matches those of recent collections. From phylogenetic analyses and morphology, it is clear that the secotioid *Nivatogastrium nubigenum* [=*Pholiota nubigena*] is nested within *Pholiota*; this species has retained ballistospores and the typical curved sterigmata for active spore dispersal.

Key words — *Abies magnifica*, biodiversity, *Strophariaceae*

## Introduction

The genus *Pholiota* (Fr.) P. Kumm. is generally characterized by (pale) yellow to brown basidiocarps with (in most species, notably excepting the type) a viscid to gelatinous, often scaly, pileus, an annulus, rusty to dark brown smooth to slightly rough spores with a germ pore, cheilocystidia and pleurocystidia (in a number of species as chrysocystidia), and typically lignicolous habit (e.g., Jacobsson 2009). Smith & Hesler (1968), in their overview of North American species of *Pholiota,* used a rather broad genus concept but a narrow species concept and gave descriptions of 205 species for North America, 163 of which were described as new. Subsequently, several of these species were shown to be synonyms of each other or to belong to other genera that even Smith & Hesler (1968) recognized as distinct, e.g., *Agaricus* L. and *Stropharia* (Fr.) Quél.

(Jacobsson 1990, 1997; Noordeloos 1999; Norvell & Redhead 2000; Redhead 1984a,b). In modern treatments of *Pholiota* for various regions in Europe with narrower genus concepts, 24–28 species are recognized (Holec 2001, Jacobsson 2009, Noordeloos 2011, Holec & Kolařík 2014, Holec et al. 2014) [excluding, among others, *Crassisporium* Matheny et al., *Flammula*[1] (Fr.) P. Kumm., *Flammulaster* Earle, *Hemipholiota* (Singer) Bon, *Hemistropharia* Jacobsson & E. Larss., *Kuehneromyces* Singer & A.H. Sm., *Meottomyces* Vizzini, *Phaeolepiota* Maire ex Konrad & Maubl., *Phaeonematoloma* (Singer) Bon, *Phaeomarasmius* Scherff., and a number of *Tubaria* species, comprising 40–50 species]. The reasons for the discrepancy in species totals between Europe and North America are multiple; it is due partly to a strong difference in both genus and species concepts and reliance on poorly documented earlier descriptions in order to be comprehensive or partly reflects variation in fresh basidiocarp characteristics leading to multiple descriptions of species. The aspect of the basidiocarps changes dramatically due to weather – the slimy species are dry during dry weather; furthermore, in the species of *Pholiota* subg. *Flammuloides* A.H. Sm. & Hesler the pleurocystidia show considerable variation in incrustation, wall thickness, and coloration among collections of the same species (see below). As a result species recognition based on morphology alone can be challenging. Many new species described by Smith & Hesler (1968) were based on only one collection, and the authors probably underestimated the variability of the species they described.

A common snowbank species in *Pholiota* subg. *Flammuloides* (with a gelatinous pileus surface and conspicuous lageniform pleurocystidia but without chrysocystidia) was regularly found in California's Red Fir (*Abies magnifica* A. Murray bis) zone in the Sierra Nevada and Southern Cascade mountains. For a number of years the fungus was considered undescribed (Arora 1986), but a scrupulous combing of Smith & Hesler's 1968 *Pholiota* monograph turned up one possible name: *Pholiota olivaceophylla*. This species was described based on one collection, occurring 'on and near very rotten Shasta fir log, Mt. Shasta, Calif. June 1954' (Shasta fir is the vernacular name for *A. magnifica* var. *shastensis* Lemmon). Besides being collected at the right time and place, the morphology also fits our unnamed species, except for the color of the lamellae. We never found olivaceous tinges in the (young) lamellae of

[1]The name *Flammula* (Fr.) P. Kumm., published in 1871, is a later homonym of *Flammula* (Webb ex Spach) Fourr. from 1868, a genus in the *Ranunculaceae;* Donk (1962) considered the latter to be invalid, but his point of view is not followed by later authors such as Jacobsson (2012). A proposal for conservation of the fungal genus *Flammula* has been put forward by Redhead (2013).

our specimens (Plate 2). Subsequently, the microscopic features of the type of *Ph. olivaceophylla* were examined and the ITS sequences of the type and recent collections were compared. Here, based on a wide sampling from different locations within California, we present a thorough description of the species with a photograph, and we place the ITS sequences in the context of the whole genus to evaluate the taxonomic position of the species.

*Pholiota olivaceophylla* is considered a snowbank fungus as described by Cooke (1944, 1955). Snowbank fungi depend on the moisture provided by the melting snow for the development of their basidiocarps, and many are able to fruit under the snow. *Pholiota olivaceophylla* starts fruiting in this way, but continues fruiting after snow melt. The fungus long known as *Nivatogastrium nubigenum* is another example of this ecological group. The snowbank fruiting habit seems to be restricted to the western North American mountains and has not been encountered in Europe. Cripps (2009) gave an overview of the more common snowbank species; with the description of *Baeospora occidentalis* L.J. Hutchison & Kropp from Utah (Hutchison et al. 2012), the number of known snowbank fungi has already increased.

## Materials & methods

Morphology—Standard methods for describing basidiocarps were applied, using the terminology of Vellinga & Noordeloos (1999). Color annotations in the macroscopical descriptions follow Kornerup & Wanscher (1967). Microscopical observations were made from dried material rehydrated in 10% ammonia. The notation [81, 4, 3] indicates that measurements were made on 81 spores in four samples in three collections; spores were observed and measured from deposits on the stipe apex, and at least 20 spores were measured per collection in side view; also for a few collections, at least 20 spores per collection were measured in frontal view. The following abbreviations are used: L = number of lamellae, l = number of lamellulae between two lamellae, avl = average length, avw = average width, Q = quotient of length and width, and avQ = average quotient. The genus name *Pholiota* is abbreviated as *Ph*. Collections are in UC, except the type collection (in MICH). Herbarium abbreviations are according to Thiers (2015, continuously updated). [For full collection information (including Genbank accession numbers) see http://mycotaxon.com/vol/130/Siegel_Table1.pdf]

DNA extraction & sequencing—Collections for this study were made specifically during the Yosemite National Park fungus survey, and during the National Forest Service surveys in the southern Cascade Range in California. We extracted DNA using a modified Sigma Extract-N-Amp kit (Sigma Aldrich, St. Louis, MO) for dried mushrooms and Whatman™ FTA™ Plant cards (Whatman Ltd) for dried tissue embedded in the cards following manufacturer's instructions. The nrITS region was amplified with the ITS1F/ITS4 primer set using an MJ PTC-100™ thermocycler (Applied Biosystems, Foster City, CA, USA) under conditions previously described (Gardes & Bruns 1993). PCR

products were cleaned using 0.5 µL of ExoSAP IT (USB Corp, Cleveland, OH, USA) per reaction and cycled at 37°C for 45 min, followed by 80°C for 15 min. Sequencing was performed using Big Dye chemistry and an ABI PRISM 3700 Genetic Analyzer (both from Applied Biosystems, Foster City, CA, USA). Sequences were edited and contigs were assembled using Sequencher 4.7 (Gene Codes Corporation, Ann Arbor, MI, USA), and deposited in GenBank.

Alignment & phylogenetic analyses—The nrITS sequences newly produced for this paper, plus all nrITS1-5.8S-ITS2 sequences of *Pholiota*, *Flammula,* and *Nivatogastrium* species and their environmental counterparts from GenBank (as of October 2013), were aligned with the program MAFFT version 7 (Katoh et al. 2002), and visually optimized. Two sequences in GenBank, GU234152 and GU234164, were excluded as they show 92% BLAST similarity with a *Conocybe teneroides* collection (JF08598), and are not close to *Pholiota*. The aligned sequence database was analyzed by maximum likelihood method (ML) using the on-line program RAxML version 7.7.1 (Stamatakis et al. 2008); 100 rapid ML bootstraps were performed, and bootstrap values are included in the ML tree of Plate 1. *Pholiota lignicola* [≡ *Kuehneromyces lignicola* (Peck) Redhead] and *Flammula* sp. (coll. UC1861000) were chosen as outgroup taxa.

## Results

The ITS alignment consists of 131 sequences (25 newly produced and 22 from California collections) and is 801 base pairs long. The resulting maximum likelihood tree shows that *Pholiota olivaceophylla* is well supported (100%) (Plate 1; see http://mycotaxon.com/vol/130/Siegel_Plate1.pdf for a larger online version). Its closest relatives in our analyses are a collection from Scandinavia labeled *Ph. "spumosa"* and the isotype of *Ph. ferrugineolutescens* A.H. Sm. & Hesler from northern coastal California. *Pholiota olivaceophylla* belongs to a clade that corresponds with the morphologically delineated subg. *Flammuloides* to which other common Californian taxa, such as *Ph. velaglutinosa* A.H. Sm. & Hesler, *Ph. highlandensis* (Peck) Quadr. & Lunghini, and *Ph. spumosa* (Fr. : Fr.) Singer belong. *Nivatogastrium nubigenum,* which forms secotioid basidiocarps, falls in the middle of subg. *Flammuloides*, close to a collection of an agaricoid *Pholiota* from Yosemite National Park and *Pholiota* sp. FJ717493 from Canada. *Flammula* is separate from *Pholiota,* as already shown by Gulden et al. (2005), and Matheny et al. (2015) in their work on various brown-spored groups, and in more wide-ranging works on *Agaricales* as a whole (e.g., Matheny et al. 2007, Moncalvo et al. 2002). Subgenera *Pholiota* and *Flammuloides* are clearly separate as well (Plate 1).

## Discussion

The coverage of the genus *Pholiota* in terms of ITS sequences is far from complete; some groups are well represented, but as a whole there is obviously much work to be done at all taxonomic levels. The goal of our phylogenetic

Plate 1. ITS maximum likelihood tree of the genus *Pholiota*. Numbers on branches are ML bootstrap values >69. Each terminal leaf is annotated as: GenBank accession; Taxon name; Herbarium accession; Location. Location abbreviations: AK = Alaska, AL = Alabama, BC = British Columbia (Canada), CA = California, EUR = Europe, Mex = Mexico, MI = Michigan, NC = North Carolina, NZ = New Zealand, Ont = Ontario (Canada), TN = Tennessee. Newly produced sequences are in bold.

analysis was not to deliver a thorough hypothesis on the evolution and phylogenetic relationships of *Pholiota* taxa, but to show the grouping and position of *Ph. olivaceophylla* and *Ph. nubigena* in general terms. As is clear from Plate 1, species concepts are in need of reconsideration, as identical sequences have been produced from collections that had been identified as different species (e.g., in the *Ph. adiposa* clade), and the same name had been applied to collections that belong to different clades (e.g., *Ph. spumosa*).

Sequencing of type collections, as started by Matheny and co-workers (in TENN), should be expanded to all species described by Smith & Hesler (1968), and neotypes and epitypes should be selected and presented with their sequence data. Holec et al. (2014) also suggested increased sampling and sequencing efforts to better understand the diversity and variability of the species.

Striking is that *Pholiota castanea* A.H. Sm. & Hesler (ITS GenBank HQ222025 from the type collection), described as the only other species in stirps *Olivaceophyllae,* from the Great Smoky Mountains National Park, is not closely related to *Ph. olivaceophylla* (Plate 1), but is close to the recently described European *Ph. chocenensis* Holec & M. Kolařík. *Pholiota castanea* and *Ph. olivaceophylla* stand out among the species in subg. *Flammuloides* because of their non-gelatinized subhymenium (Smith & Hesler 1968).

Based on an analysis of a 6-locus database of the *Agaricales* as a whole, the secotioid *N. nubigenum* is a sister taxon to *Pholiota squarrosa* (Vahl : Fr.) P. Kumm., the only agaricoid *Pholiota* species included in that analysis (Matheny et al. 2007); it is a sister taxon to *Pholiota multicingulata* E. Horak in another study of the *Agaricales* based on a 4-locus database (Matheny et al. 2015). In the present ITS analysis, *Ph. nubigena* (as *Nivatogastrium nubigenum* in Plate 1) clearly nests within *Pholiota* subg. *Flammuloides*. Redhead (2014) proposed the new combination of this species in *Pholiota*.

## Taxonomy

***Pholiota olivaceophylla*** A.H. Sm. & Hesler, N. Am. Species *Pholiota*: 236. 1968.
Plates 2–6

Pileus (30–)40–80(–100) mm, convex to broadly convex, becoming applanate, occasionally wavy or lobed in age; margin inrolled when young, becoming even, undulating in age, often with veil remnants when young; surface smooth, viscid when wet, becoming tacky, often with debris stuck to it, shiny when dry, creamy-orange, pale orange-buff to pale orange-tan when young, becoming creamy-buff to tan, often with darker orange-tan streaks or patches; slime pale orange. Lamellae, L = about 50–60, l = 1–3, close to subdistant, adnate with decurrent tooth, 7–10 mm wide, pale tan to buff (5B3–5C4) when young, becoming tan, light brown to pale olive-brown, with even concolorous

Plate 2. *Pholiota olivaceophylla* (UC1999285). Photo by Noah Siegel

edges. Stipe 50–90 × 10–18 mm, equal or enlarged at base, whitish when young, covered with pale orange-buff slimy veil except for apex, becoming off-white to dingy tan with pale orange streaks, dry and white above veil, becoming dingy tan in age, at base covered with fuzzy white mycelium that binds to organic matter, stuffed when young, becoming hollow in age. Partial veil a mucilaginous cortina, breaking up and leaving remnants around pileus margin and a faint very pale orange ring that becomes brown with spores. Context white to pale cream in pileus, watery-white to pale tan in stipe, becoming tan to pale brown. Odor musty, herbaceous. Taste mild. Chemical reactions: 5% KOH on pileus pale yellowish orange, on upper stipe orange, little reaction on lower stipe, on pileus context bright orange, becoming orange-brown, on stipe context orangish. Spore print color medium brown.

Basidiospores in side view [200, 10, 10] 5.9–8.3 × 3.5–4.4 µm, avl × avw = 6.4–7.3 × 3.9–4.1 µm, Q = 1.45–1.95, ellipsoid to oblong, some slightly phaseoliform, in frontal view [40, 2, 2] 6.0–7.6 × 3.4–4.4 µm, avl × avw = 6.4–6.8 × 4.0–4.2 µm, Q = 1.4–1.9, avQ = 1.55–1.8, relatively thin-walled; germ pore and hilar appendage inconspicuous. Basidia 17–29 × 5–8 µm, 4-spored, with basal clamp connection. Lamella edge sterile. Cheilocystidia 25–65 × 8–15 µm, with 4–6 µm wide neck, lageniform, utriform, or clavate, a few similar in shape and size to pleurocystidia, variously incrusted, with coarse material or

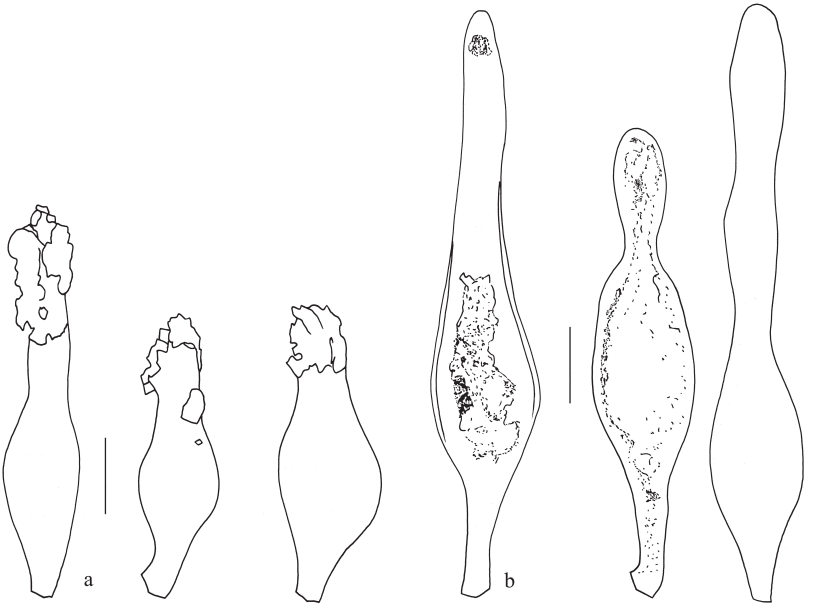


Plate 3. *Pholiota olivaceophylla*. a. Cheilocystidia; b. pleurocystidia (both from UC UC1999268). Scale bars = 10 µm. Drawing by ECV.

with some small pieces, in some collections with yellow contents in ammonia. Pleurocystidia 48–91 × 10–17.5 µm, with 4–10 µm wide neck, lageniform, very abundant, protruding from hymenium, variable in size and ornamentation, yellow in ammonia in some collections, with or without an apical covering of crystalline material, or with amorphous matter inside, or without any inclusions, with slightly thickened walls in lower part of neck. Hymenophoral trama not pigmented. Subhymenium not gelatinized. Pileipellis an ixocutis of cylindrical non-colored hyphae, 2–5 µm wide; subpellis a cutis of cylindrical to slightly inflated hyphae, 5–10 µm wide with brown walls. Stipitipellis a cutis of cylindrical colourless hyphae, 4–11 µm wide, without caulocystidia. Clamp connections present in all tissues.

Specimens examined: **USA**: **California**, **Siskiyou Co.**, Modoc National Forest, north slope of Black Mountain, near junction of Forest Road 44N33 & 44N12, in *Abies magnifica* & *A. concolor* forest, 29 May 2012, E.C. Vellinga (UC 1999279); in *A. magnifica* & *A. concolor* forest on small branches and thick duff near melting snow, 29 May 2012, N. Siegel (UC 1999281; GenBank KC122883); in *A. magnifica* & *A. concolor* forest on conifer wood, 29 May 2012, E.C. Vellinga (UC 1999285; GenBank KC122888); in *A. magnifica* & *A. concolor* forest on conifer wood & twigs, 29 May 2012, E.C. Vellinga (UC 1999276); in *A. magnifica* & *A. concolor* forest, 29 May 2012, N. Siegel (UC 1999280);

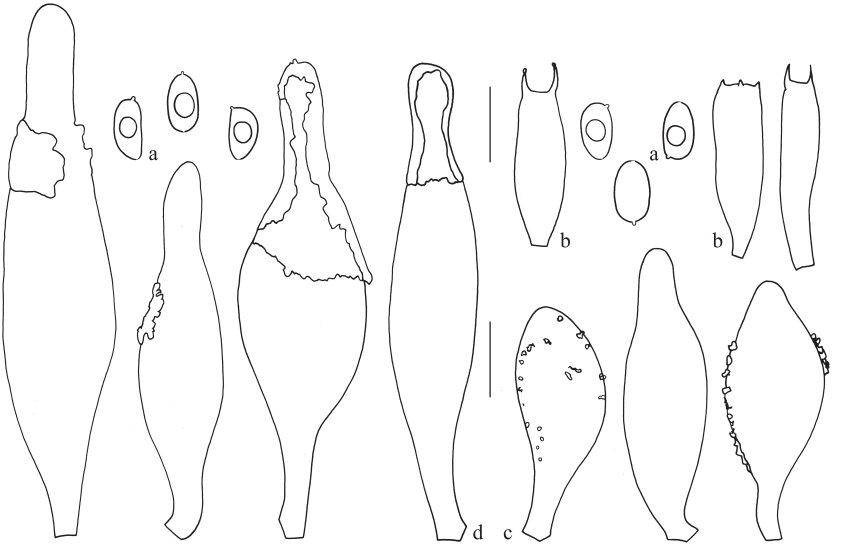


Plate 4. *Pholiota olivaceophylla*. a. Spores; b. basidia; c. cheilocystidia; d. pleurocystidia (all from UC1999272). Scale bars = 10 μm. Drawing by ECV.

Mount Shasta, on and under rotten *A. magnifica* log, 1 June 1954, W.B. Cooke (MICH 290502, holotype; GenBank KF878381); Mount Shasta, near Clear Creek Trailhead, in *A. magnifica* forest, 28 May 2012, E.C. Vellinga (UC 1999277); Trout Creek area, in *A. magnifica* and *A. concolor* forest, on conifer wood and twigs, 28 May 2012, E.C. Vellinga (UC 1999283; GenBank KC122889); Six Shooter Butte, in *A. magnifica* forest, on conifer wood, 27 May 2012, E.C. Vellinga (UC 1999278); Shasta National Forest, Trout Butte area, 28 May 2012, N. Siegel (UC 1999284; GenBank KC122878); **Tuolumne Co.**, Yosemite National Park, Crane Flat, north of gas station, in mixed coniferous forest, on conifer wood, 4 June 2010, N. Siegel (UC 1999268; GenBank KC122882); Tamarack Flat Road near Tioga Road, 37.7966°N 119.8655°W, in *A. magnifica* forest, on conifer wood, 5 June 2010, D. Viess (UC 1999272; GenBank KC122885); **Mariposa Co.**, Yosemite National Park, Glacier Point Road, 37.67333°N 119.6523°W, in mixed coniferous forest, 30 May 2010, M. Schubert (UC 1998508; GenBank KC122894); Glacier Point Road, Summit Meadow, 37.6650°N 119.6997°W, in *P. jeffreyi*, *P. lambertiana*, & *Abies* forest, on litter, 30 May 2012, N.H. Nguyen (UC 1998643; GenBank KC122895).

Habitat & distribution—Solitary, scattered, or in small groups and clusters on small buried branches, woody debris, thick duff, or well rotted logs, in *Abies concolor* (Gordon) Lindl. ex Hildebr. and *A. magnifica* forests at 1700–2200 m asl, fruiting near melting snowbanks or areas with snow cover, occasionally fruiting under snow, May–June. Widespread in the Sierra Nevada and southern Cascades in California.

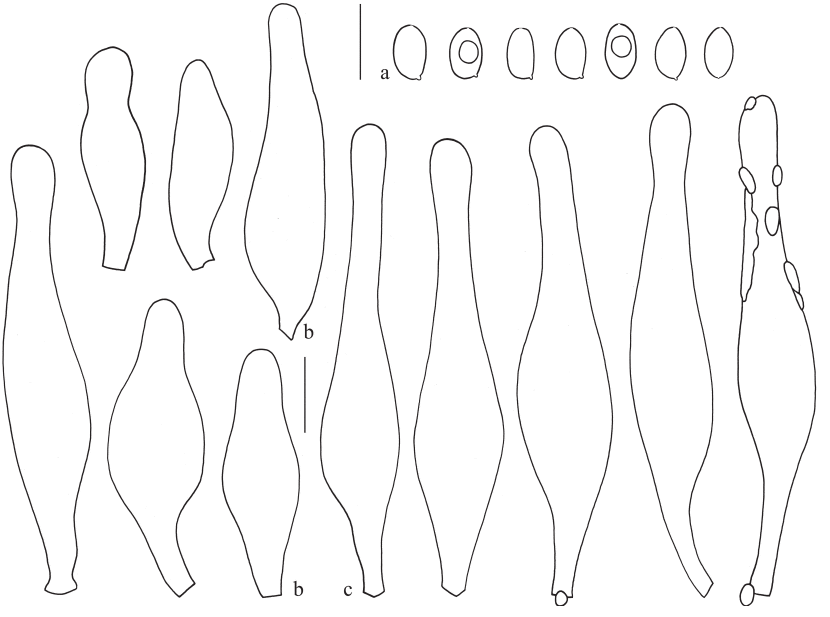


Plate 5. *Pholiota olivaceophylla.* a. Spores; b. cheilocystidia; c. pleurocystidia (all from UC1998643). Scale bars = 10 µm. Drawing by ECV.

The type collection was in good condition, and the dried specimens of recent collections look very similar. The following characters were noted for the type collection (Plate 6):

Spores [20, 1] 6.4–7.8 × 3.4–4.7 µm in side-view, avl × avw = 7.0 × 3.9 µm, Q = 1.67–1.89, avQ = 1.8, elongate, slightly phaseoliform, pale brown, with inconspicuous germ pore and hilar appendage. Basidia 20–23 × 5.0–6.5 µm, 4-spored, with basal clamp connection. Cheilocystidia present, difficult to observe, lageniform. Pleurocystidia abundant, 63-80 × 11–16 µm, lageniform, with 15–35 µm long cylindrical, rarely ventricose neck, often slightly pinched in near the wider part, with or without yellowish contents, slightly thick-walled.

Additional specimens examined:

***Flammula* sp.: USA: California, Mariposa Co.**, Yosemite National Park, White Wolf campground, 37.869383°N -119.646585°W, in *A. concolor* and *P. contorta* forest, on conifer wood, 18 Aug. 2010, P.G. Werner (UC 1860901; Genbank KC122893); Yosemite National Park, Glacier Point Road, 37.7065°N -119.5890°W, in *Pinus contorta* forest, 29 Oct. 2011, L. Rosenthal (UC 1861000; Genbank KC122880).

***Pholiota* cf. *brunnescens*: USA: California, Mariposa Co.**, Yosemite National Park, Mariposa Grove loop trail, 37.50568°N -119.60847°W, in mixed coniferous forest,

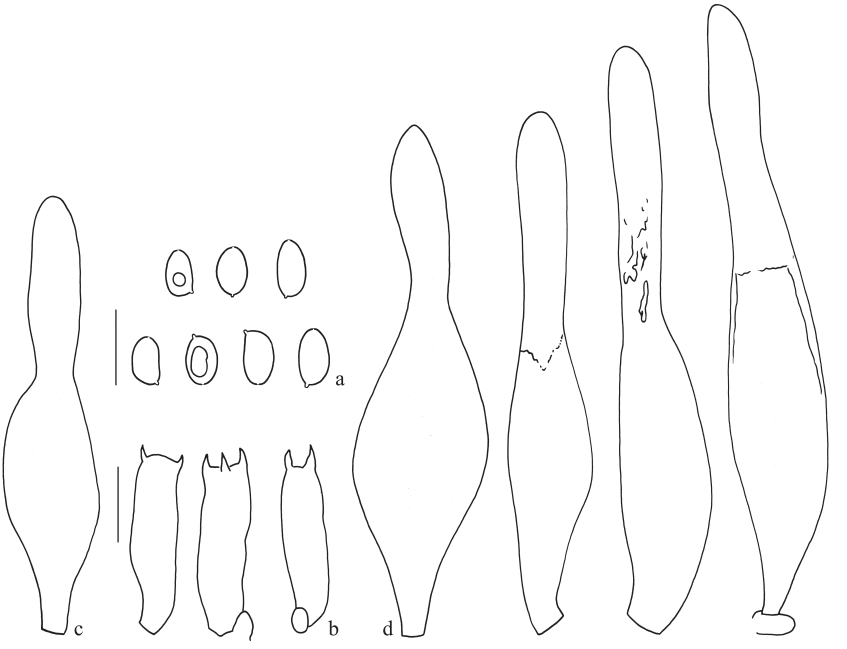


Plate 6. *Pholiota olivaceophylla.* a. Spores; b. basidia; c. cheilocystidium; d. pleurocystidia (all from holotype). Scale bars = 10 μm. Drawing by ECV.

29 May 2010, N.H. Nguyen (UC 1998624; Genbank KC122891); **Tuolumne Co.,** Yosemite National Park, Tamarack Flat Road, 37.7966°N -119.8655°W, in *P. ponderosa*, *Pseudotsuga menziesii* & *Calocedrus decurrens* forest, N. Siegel, 5 June 2010 (UC 1999269; Genbank KC122892).

***Pholiota* cf. *decorata*: USA: Alaska, Anchorage Co.,** Girdwood, Iditarod Trail, in forest with *Picea sitchensis* and *Tsuga,* 31 Aug. 2012, E.C. Vellinga 5567b (UC 1999442; Genbank KF878380).

***Pholiota highlandensis*: USA: California, Mendocino Co.,** Mendocino, off Wheeler Street, on burnt ground under *Pinus,* 2 Jan. 2013, N. Siegel (UC 1999437; Genbank KF878376).

***Pholiota lenta* s.l.: USA: California, Yuba Co.,** Bullard's Bar Recreation Area, Hornswaggle Campground, 39.4146°N -121.1205°W, mixed conifer forest, on coniferous wood, 10 Dec. 2011, E.C. Vellinga (UC 1999282; Genbank KC122876).

***Pholiota mixta*: USA: Alaska, Kenai Peninsula,** Hope, along Palmer Creek Road, 3 Sept. 2012, E.C. Vellinga 5580b (UC 1999441; Genbank KF878377).

***Pholiota* sp.: USA: Alaska, Kenai Peninsula,** Hope, along Palmer Creek Road, 3 Sept. 2012, E.C. Vellinga 5578b (UC 1999439; Genbank KF878378); **California**, Yosemite National Park, Highway 120, in *A. magnifica* forest, on conifer wood, 30 Sept. 2011, D. Rust (UC 1999274; Genbank KC122881); **North Carolina,** Mount Mitchell State Park, on conifer wood, 22 Sept. 2012, D. Viess (UC UC 1999438; Genbank KF878379).

***Pholiota spumosa*: USA: California, Alameda Co.,** Berkeley, along Euclid Avenue, on *Pinus* bark chips in garden, 18 March 2012, E.C. Vellinga (UC 1999286; Genbank KC122886); **Mariposa Co.**, Yosemite National Park, Wawona Meadow Loop Trail, 37.523056°N -119.636111°W, on buried conifer wood, 29 May 2010, E.P. Blanchard (UC UC 1998527; Genbank KC122879).

***Pholiota terrestris*: USA: California, Marin Co.,** Point Reyes National Seashore, Olema Trail, 37.9917°N -122.7580°W, in *Ps. menziesii* & hardwood forest, 9 Dec. 2006, K. Takeoka (UC 1859859; Genbank KC122896); Point Reyes National Seashore, Bayview Trail, 38.0608°N -122.8564°W, in *P. muricata* forest, 29 Dec. 2007, Aletheap (UC 1860187; Genbank KC122887).

***Pholiota velaglutinosa:* USA: California, Marin Co.,** Point Reyes National Seashore, Mount Vision, 38.1016°N -122.8947°W, in *P. muricata* forest, 10 Dec. 2005, Murray (UC 1859567; Genbank KC122877).

Comments—The data noted from the type collection concur with those given by Smith & Hesler (1968) and fit well the modern data for the collections from California's mountain ranges. An image of A.H. Smith's original notes can be found in Mycoportal (http://mycoportal.org).

*Pholiota olivaceophylla* commonly fruits in May and June during and just after snowmelt in the *Abies* forests of the Sierra Nevada and Cascade ranges. It can easily be distinguished from the other common species in *Pholiota* subg. *Flammuloides* fruiting at the same time in the mountains. For example, *Ph. highlandensis* and *Ph. brunnescens* A.H. Sm. & Hesler grow on recent burns, have smaller basidiocarps and deeper brown, thick-walled spores. Species in the *Ph. spumosa* complex enjoy bright yellow colors in the basidiocarps, and have brown thick-walled spores with a distinct germ pore, which are similar in size to those of *Ph. olivaceophylla*.

The European species *Ph. elegans* Jacobsson comes close in overall appearance, but differs in habitat (mainly in virgin, often deciduous, forests and fruiting in autumn), and slightly smaller, distinctly phaseoliform-amygdaloid spores, 5.0–6.7(–7.0) µm long (Holec 2001).

The North American species in *Pholiota* subg. *Flammuloides* are in serious need of revision, and interpretation of many species described by Smith and Hesler (1968) is challenging. However, some species yield to interpretation and appear to be close to *Ph. olivaceophylla* in their pale colors, but differ in critical characters: the pale species *Ph. flavopallida* A.H. Sm. & Hesler has spores 5–6 µm long, and *Ph. agglutinata* A.H. Sm. & Hesler has a white veil, and was found in late summer. There are, as far as we know, no other spring-fruiting mountain-dwelling species described. McClenaghan (1991) in her overview of northern California species gave a relatively short description of *Ph. olivaceophylla* based on one collection (which we have not studied), and stressed the olivaceous lamellae that turn to dark brown with age, characters we did not observe in the

many specimens we collected. Other characters (including the location and the time of collecting) do fit with our concept of *Ph. olivaceophylla*.

The pleurocystidia of *Ph. olivaceophylla* are highly variable in size, in contents, and in ornamentation among collections (Plates 3–6); how this is influenced by age of the basidiocarps and environmental variables is unknown. There is no overlap in pleurocystidium size among the collections with the shortest and those with the longest pleurocystidia. Constant are the relatively thin walls and relatively pale brown color of the spores under the microscope, and inconspicuous germ pore and hilar appendage. Spore color is a much better character at species level than pleurocystidium shape and size, but it is a qualitative character, and thus harder to assess.

***Pholiota nubigena*** (Harkn.) Redhead, Index Fungorum 148: 1. 2014. Plate 7

≡ *Secotium nubigenum* Harkn., Bull. California Acad. Sci. 1(4): 257. 1886.

≡ *Nivatogastrium nubigenum* (Harkn.) Singer & A.H. Sm., Brittonia 11: 224. 1959.

Comments—*Pholiota nubigena* shares both the hallmarks for subg. *Flammuloides* and the habitat with *Ph. olivaceophylla*. The pleurocystidia are

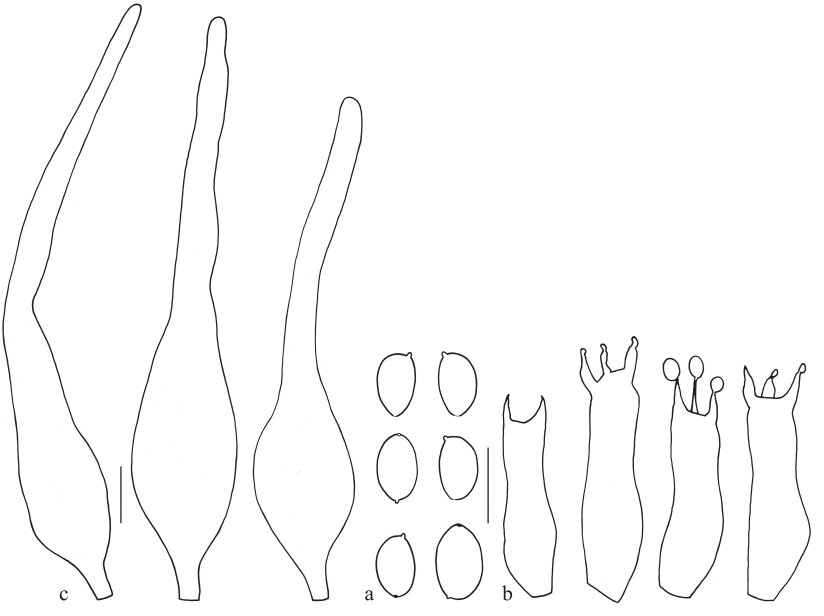


Plate 7. *Pholiota nubigena.* a. Spores; b. basidia; c. pleurocystidia (all from UC1998744). Scale bars = 10 μm (note different scale for c than in the other figs.). Drawing by ECV.

numerous and lageniform with a very long neck without yellow inclusions (chrysocystidia are absent), the spores are larger than those of *Ph. olivaceophylla* (based on our observations on collection UC 1998744 [25, 1, 1] 7.8–10.8 × 4.9–6.2 µm in side-view), with a medium brown, medium thick wall, a distinct hilar appendage, and a hardly visible germ pore (Plate 7a).

The spores are asymmetrical in side view, and the basidia have sterigmata typical for ballistospore dispersal (Plate 7b). *Pholiota nubigena* grows, like *Ph. olivaceophylla*, on conifer wood, and is widespread in the western North American mountains, with records from the southern Sierras northwards into Idaho and the Rocky Mountains in Montana (http://mycoportal.org retrieved 12 February 2015).

Specimen examined: **USA**: **California**, **Mariposa Co.**, Yosemite NP, Glacier Point Road, 37.6687°N 119.6113°W, M.G. Wood, 30 May 2010, M.G. Wood (UC 1998744).

Phylogenetically *Ph. nubigena* falls in the middle of subg. *Flammuloides*, and a relationship with *Pholiota* — which has been proposed in the past, both prior to (e.g. Singer & Smith 1959, Smith & Hesler 1968) and subsequent to molecular analyses (Matheny et al. 2007, 2015) — is again confirmed here.

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